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THE AURICULATE-LEAVED SPECIES OF LESQUERELLA (CRUCIFERAE)

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AN intensive study of the most easterly species of the genus *Lesquerella* has raised a number of problems regarding the taxonomy of those with auriculate cauline leaves. With the possible exception of *L. lasiocarpa*, these are all more closely related to each other than to other species of the genus and should be formed into a separate section or subgenus. There is now definite proof that the flat-podded *L. Lescurii* is genetically very closely related to the very unlike globose-podded *L. densipila*. They cross freely in the field (Rollins, 1954) and can be readily crossed in the laboratory, producing highly viable seeds. Second generation offspring retain the high fertility of the F_1, so that there appears to be little or no bar to free gene exchange between them. The total evidence (to be presented elsewhere) shows without question that *L. Lescurii*, though singular in many of its characteristics, should not form a monotypic section as maintained by Payson (1922) in his monograph of the genus. The earlier treatment of Watson (1888) in which *L. Lescurii* is associated with *L. auriculata* and *L. grandiflora* is preferable.

The differentiation of *Lesquerella* in the Central Basin of Tennessee resulting in such morphologically divergent species as *L. Lescurii*, *L. densipila* and *L. perforata* has posed questions as to their origin and nearest relatives within the genus. Where did these Tennessee Lesquerellas come from and by what migratory route did they get there? The genus in large part is southwestern

and Mexican in distribution with a heavy concentration of species in Texas. However, there are a goodly number in the Rocky Mountain area and several species in South America. But for the relatives of the Tennessee species, we need to look no farther west than Texas and Oklahoma. There, among the three possible species, *L. auriculata* appears to be the most likely progenitor of the more easterly species. Not only does it agree in many characteristics with the Tennessee and Alabama species under consideration but the chromosome number of n = 8 is the same. *L. grandiflora*, the other possible Texas relative, has n = 9.

The discovery of a new species, *L. lyrata*, in northwestern Alabama is significant in connection with the problems posed above. This species, lying geographically and morphologically between *L. densipila* of Tennessee and *L. auriculata* of Oklahoma and Texas, fills a gap as nearly as one could ask for it. *L. lyrata* provides the proper evolutional step from *L. auriculata* to *L. densipila* as well as a possible remnant of a more or less continuous distribution pattern that must have connected the Tennessee and southwest species in a past era. It is interesting that *L. lyrata* should only now be found and furthermore that *L. gracilis*[1] should be discovered in Mississippi for the first time.

Lesquerella as a whole is under study, and it is hoped that a monograph of this interesting genus may eventually be presented. The present paper deals with only the auriculate-leaved species. The herbarium citations follow the symbols of Index Herbariorum (1954). I am indebted to Dr. L. O. Gaiser and Mrs. Winslow Briggs for making the chromosome counts given at the end of each description in those instances where it is known. Dr. Elsie Quarterman of Vanderbilt University has kindly assisted by providing information about the Central Basin of Tennessee and by participating in the field work, for which I am grateful.

[1] Last April, in company with Mr. George R. Cooley and Dr. James D. Ray, Jr., I examined a large population of *L. gracilis* (Hook.) Wats. growing on heavy black prairie land just north of Okolona in Chickasaw County, Mississippi. Here the plants were as thoroughly at home as on the black-land prairies of Texas. Thanks to the efforts of Dr. Ray, Mr. Cooley, and Mr. L. J. Brass, there are now three known stations for *L. gracilis* in Mississippi, the southernmost in Lowndes County and the northernmost in Pontotoc County, all on the "prairie strip." To my knowledge, the genus *Lesquerella* has not been previously reported from either Mississippi or Alabama.

KEY TO THE SPECIES

A. Pedicels recurved; siliques slightly compressed to flattened contrary to septum; filaments not dilated at base; cauline leaves nonauriculate to obscurely auriculate, not clasping the stem . . . . . 1. *L. lasiocarpa.*
A. Pedicels ascending; siliques globose, subglobose, pyriform, or flattened parallel to septum; filaments dilated at base; cauline leaves markedly auriculate and clasping the stem.
B. Siliques strongly flattened parallel to septum; valves pubescent with a mixture of large bulbous-based trichomes and an understory of small branched trichomes; flowers yellow . . . . . 2. *L. Lescurii.*
B. Siliques globose, subglobose or pyriform, not flattened; valves glabrous or uniformly pubescent with simple or forked trichomes; flowers yellow or white.
C. Flowers yellow; siliques globose or subglobose; septum complete.
D. Siliques densely pubescent with minute simple or forked trichomes; styles pubescent; plants of Tennessee . . . . . 3. *L. densipila.*
D. Siliques glabrous; styles glabrous; plants of Alabama, Oklahoma, and Texas.
E. Ovules 4–8 in each silique, septum dense, opaque; stigma scarcely expanded; siliques less than 3 mm. high, depressed globose . . . . . 4. *L. lyrata.*
E. Ovules 12–20 in each silique; septum less dense, translucent; stigma markedly expanded; siliques 4–8 mm. high, globose to elliptical.
F. Lower stems hirsute with spreading simple trichomes; lower cauline leaves markedly auriculate; petals 4–5 mm. wide; infructescences dense . . . . . 7. *L. auriculata.*
F. Lower stems pubescent with appressed branched trichomes; lower cauline leaves not auriculate; petals 6–9 mm. wide; infructescences lax, greatly elongated . . . . . 8. *L. grandiflora.*
C. Flowers white; siliques pyriform or depressed globose to somewhat didymous; septum perforate.
G. Siliques densely hirsute, slightly didymous to depressed globose; valves glabrous on interior; styles hirsute . . . . . 5. *L. stonensis.*
G. Siliques glabrous to very sparsely hirsute, pyriform; valves densely pubescent on interior; styles glabrous . . . . . 6. *L. perforata.*

1. **Lesquerella lasiocarpa** (Hook. ex Gray) Watson, Proc. Amer. Acad. **23:** 251, 1888.

Annuals, biennials or perennials; stems several to numerous, slender, decumbent to procumbent, pubescent with branched trichomes or a combination of branched and simple spreading trichomes, 1–5 dm. long; basal leaves petiolate, oblanceolate in outline, variable, sinuate dentate to somewhat lobed or incised, 3–10 cm. long, 1–3 cm. wide, densely pubescent with small branched trichomes or a mixture of these and large trichomes; cauline leaves sessile, narrowed toward base, varying from nonauriculate to barely auriculate or with definite auricles present, sinuate dentate to incised, obovate elliptical or oblong in outline, densely pubescent, 1–4 cm. long, 0.5–2 cm. wide; infructescence lax; pedicels slender, recurved in fruit, not expanded toward summit, densely pubescent, 1.5–

2.5 cm. long; sepals green, pubescent with small branched trichomes to hirsute, linear-oblong, nearly acuminate, 4–5 mm. long, 1.5–2 mm. wide; petals broadly obovate, 6–8 mm. long, 4.5–5.5 mm. wide, light yellow, often drying purplish, blade nearly orbicular, limb very short; anthers sagittate, 2–3 mm. long; filaments not dilated at base, barely exceeding anthers in length; glands formed into horn-like projections at the bases of the filaments; siliques sessile, definitely flattened contrary to the partition to only slightly flattened, orbicular in outline to elliptical or cordate; densely pubescent with a mixture of small branched and large simple trichomes or with the simple trichomes absent, 5–9 mm. long, 4–9 mm. wide; style 1–1.5 mm. long; stigma expanded; replum oblong to nearly elliptical; septum transparent; ovules 8–14 in each locule; funiculi attached to septum at base; seeds nearly orbicular, slightly longer than broad, margined, ca. 1.5 mm. long; cotyledons accumbent.

Key to the Varieties

Siliques hirsute with large simple trichomes as well as being pubescent with an understory of small branched trichomes.
Plants annual; caudex not noticeably thickened; cauline leaves scarcely cuneate at base, barely auriculate to definitely so; low elevations in Texas and coastal eastern and northeastern Mexico.
Siliques orbicular to elliptical in outline; leaf-lobes acute to acuminate .....1a. var. *lasiocarpa.*
Siliques cordate in outline; leaf lobes rounded to obtuse, plants of Mexico .....1c. var. *ampla.*
Plants biennial or perennial; caudex thick; cauline leaves cuneate at base, nonauriculate; mountains and foothills of northeastern Mexico.....
.....1d. var. *heterochroma.*
Siliques pubescent with small branched trichomes only..1b. var. *Berlandieri.*

1a. **L. lasiocarpa** var. **lasiocarpa.**

Vesicaria lasiocarpa Hook. ex. Gray, Smithson. Contrib. **5:** 13. 1853.

Synthlipsis Berlandieri var. *hispida* Watson, Proc. Am. Acad. **17:** 321. 1882.

Alyssum lasiocarpa Kuntze, Rev. Gen. Pl. **2:** 931. 1891. Type seen at Kew, but there is no indication of place of collection on the type sheet. Gray, l.c., says, "between Bexar and Trinity River, May, 1828, Berlandier (in herb Hook.)."

Texas: Rio Frio north of Dilley, Frio Co., *Painter, Lucas & Barkley 14206* (MO, TEX); 3 mi. south of Dilley, La Salle Co., *Painter & Barkley 14305* (TEX); Rockport, Arkansas Co., *Tharp s.n.* (GH); Corpus Christi, Nueces Co., *Tracy 9348* in part (NY); same locality, *E. J. Palmer 11215* (MO, TEX); same locality, *Heller 1405* (GH, MO); Bishop, Nueces Co., *Young s.n.* (TEX); Alice, Jim Wells Co., *E. J. Palmer 11259* (MO, TEX); San Diego, Duval Co., *Croft s.n.* (GH, NY); Apache Ranch, ca. 40 mi. s.w. Catarina, Webb Co., *Blair et al. 48-500* (TEX); 6 mi. n. Laredo, Webb Co., *K. M. & M. C. Wiegand 750* (GH); 6 mi. w. of Aguilares, Webb Co., *Tharp et al. 51-1693* (TEX); King Ranch, Kleberg Co., *M. C. Johnston 5410* (TEX); Kingsville, Kleberg Co., *High 57* (MO); 4½ mi. e. of Hebbronville, Jim Hogg Co., *M. C. Johnston 54124* (OKLA, TEX); Donna,

Hidalgo Co., *Clover 624* (NY); 3 mi. n. of Edinburg, Hidalgo Co., *Painter & Barkley 14448* (TEX); s. of Raymondville, Willacy Co., *Gentry 52–653* (TEX); w. of Holly Beach, Cameron Co., *M. C. Johnston 54201* (TEX); w. of Brownsville, Cameron Co., *Hansen 321* (GH, MO, NY, TEX).

Mexico: Hacienda el Carrizo, Nuevo León, *Pringle 10236* (GH, NY); 23 mi. n. of Sabinas Hidalgo, Nuevo León, *Webster & Barkley 14591* (TEX); Sierra de San Carlos, Tamaulipas, *Berlandier 3101* (GH): Laredo, Tamaulipas, *Berlandier 157* (GH); 16 mi. s. of Nuevo Laredo, Tamaulipas, *Heard 2* (TEX); San Lorenzo de Leguna, 70 mi. s.w. from Parras, Coahuila, *E. Palmer 26* (GH, type of *Synthlipsis Berlandieri* var. *hispida*).

1b. **L. lasiocarpa** var. **Berlandieri** (Gray) Payson, Ann. Mo. Bot. Gard. **8:** 139. 1922.

Synthlipsis Berlandieri Gray, Bot. Mex. Bound. Surv. 34. 1859.

Texas: Corpus Christi, Nueces Co., *Tracy 9348* (GH, MO, NY in part); Sanz Ranch, Willacy Co., *M. C. Johnston 54547* (TEX); San Juan, Hidalgo Co., *Parks 18003* (GH). **Mexico:** Matamoros, Tamaulipas, April, 1836, *Berlandier 3017* (GH, type; MO); same location, *Berlandier 710, 778, 1517, 2127, 2198, 3102* (GH);

1c. **L. lasiocarpa** var. **ampla** Rollins, var. nov.

Herba annua; foliis obtusis amplis; siliquis cordatis.

Mexico: vicinity of Victoria, Tamaulipas, Feb. 1 to Aptil 9, 1907, *E. Palmer 41* (GH, type; NY, isotype); vicinity of Pueblo Vieja, Vera Cruz, 2 kilo. s. of Tampico, *E. Palmer 366* (GH).

1d. **L. lasiocarpa** var. **heterochroma** (Watson) Rollins, comb. nov.

Synthlipsis heterochroma Watson, Proc. Amer. Acad. **17:** 321. 1882.

Mexico. Nuevo León: Guajuco, 27 mi. s.e. from Monterrey, March, 1880, *E. Palmer 33* (GH, type); Villa de Santiago, *Leavenworth 120* (GH); Linares, *I. C. & E. M. Frye 2522a* (GH); 12 mi. e. of Monterrey, *Barkley 14354* (TEX).

Lesquerella lasiocarpa is tremendously variable. Not only can one find a great range in the size of individual plants but every part of the plant seems to run through a rather wide range of variation. For example, this species has been commonly thought of as having siliques that are rather markedly flattened contrary to the partition, the resulting shape of the replum being narrowly oblong. However, the actual amount of flattening varies all the way from the rather strongly flattened type to siliques that are just short of being round. In the latter type, the replum is broadly elliptical to nearly round. Other characters are not noticeably correlated with the degree of flattening. Many of the plants collected are obviously

annuals, but some, as in the type of Watson's *Synthlipsis heterochroma* and other specimens from Nuevo León, seem to be perennials. Unfortunately, I have had no field experience with this particular species and can only attempt to interpret the specimens.

Although quite definitely a *Lesquerella*, this species has certain features in common with the monotypic genus *Synthlipsis* and suggests a possible ancient connection between the two genera. If this view gains further support as evidence concerning the phylogeny of the Cruciferae is accumulated, it would point to a southern, perhaps Mexican, origin for the genus *Lesquerella*. This idea is in immediate conflict with a widely held view that *Lesquerella* is related to and probably originated from either *Vesicaria* or *Alyssum* of the Old World.

The varieties of *L. lasiocarpa* are not especially marked except with relatively minor characters. Variety *Berlandieri* lacks large simple trichomes on the fruits and has a reduced number elsewhere on the plants. I am not sure that this is a natural taxon for it seems to occur within the range of var. *lasiocarpa* and has even been collected at the same location. Variety *ampla* is more southerly in its range than the other varieties and marks a trend toward cordate-shaped fruits and large blunt leaves. The simple trichomes on the fruits are not so pronounced as in var. *lasiocarpa* where they are frequently large, stiff and with a bulbous base. Payson did not recognize var. *ampla* as separable from var. *lasiocarpa* although he had available to him the same collections that I have studied. However, the Gray Herbarium specimen, which he did not see, is the one with mature fruits where the cordate shape is strongly evident.

In var. *heterochroma* appears a trend of development not seen in other varieties, that of a perennial caespitose habit. The specimens so far collected all have a comparatively thick caudex. A note by one collector (Barkley) indicates that the plants were taken near a brook, suggesting a moist habitat. All collections appear to have come from above one thousand feet in elevation. The other varieties are low elevation plants occurring mainly on the Gulf coastal plain.

Although four varieties are recognized in *L. lasiocarpa*, the present taxonomic treatment leaves considerable to be desired.

Not only is some explanation for the tremendous variation needed but there are trends of differentiation observable, for example that toward globose siliques, that require a more adequate explanation than can be surmised from specimens alone. A genetical and cytological study of this species is definitely needed and would contribute profitably to an understanding of the role of *L. lasiocarpa* in the phylogeny of the genus as a whole.

The cauline leaves of some plants of *L. lasiocarpa* are non-auriculate; in others they are slightly auriculate; and in some, definite auricles are present. The questions follow naturally as to whether *L. lasiocarpa* should be included with the definitely auriculate species as in the present treatment and whether it is more closely related to them than to other species of the genus. There is little to go on at present to provide answers to these questions except to say that *L. lasiocarpa* is as nearly in place with the auriculate species as with any group of species in the genus.

2. **Lesquerella Lescurii** (Gray) Watson, Proc. Amer. Acad. **23:** 250. 1888.

Vesicaria ? Lescurii Gray, Manual Bot. ed. 2, 38. 1856.
Alyssum Lescurii Gray, Manual Bot. ed. 5, 72. 1867.

Annual; stems several to numerous, erect or decumbent, simple or usually branched, hirsute below, densely pubescent with branched trichomes above and below, 1–3 dm. long; basal leaves petiolate, lyrate, deeply lobed, 3–7 cm. long, 5–20 mm. wide, hirsute below with mostly simple trichomes, coarsely pubescent above with a mixture of large simple and smaller branched trichomes, lateral lobes remote; cauline leaves sessile, auriculate, dentate, broadly oblong to ovate, coarsely pubescent with large simple and smaller branched trichomes, upper leaves often lacking the simple trichomes 0.5–2 cm. long, 3–10 mm. wide; pedicels divaricate, nearly straight, densely pubescent with coarse branched trichomes, 8–15 mm. long, not expanded at summit; sepals coarsely pubescent, yellowish at anthesis, broadly oblong, 3–4 mm. long, 1.5–2 mm. wide, outer pair slightly saccate, inner pair flat at base; petals yellow, obovate, rounded to slightly emarginate at apex, gradually narrowed to base with no sharp differentiation into blade and claw, 5–7 mm. long, 3.5–4.5 mm. wide; glandular tissue in a continuous mold subtending the filaments, surrounding the attachment point of single stamens; filaments dilated at base, 2.5–3.5 mm. long; anthers oblong, ca. 1 mm. long; siliques sessile, strongly flattened parallel to septum, orbicular to slightly longer than broad, 4–6 mm. long, 3–4 mm. wide, valves coarsely and densely pubescent on the exterior with large simple bulbous-based trichomes

and an understory of small branched trichomes, sparsely pubescent with minute branched trichomes on the interior; septum complete, dense; replum thick, glabrous; style glabrous, 1.5–2 mm. long; stigma greater in diameter than the style in dried material, the same diameter as the style on the growing plant; ovules 2–4 in each locule; funiculi attached to septum at base only; seeds flattened, prominently margined, nearly orbicular in outline to slightly longer than broad, 2–2.8 mm. long, 1.5–2 mm. broad; cotyledons accumbent. N = 8. Plate 1207.

L. Lescurii is limited in distribution to central Tennessee. The following specimens, supplementing those cited earlier (Rollins, 1952), show a considerably wider range than was formerly known.

Tennessee. Summer County: 4.5 mi. e. of Gallatin, *Deam 61336* (DEAM). Wilson County: 2 mi. n. of Green Hill, *Rollins 5309* (GH). Rutherford County: Stewart's Creek, ½ mi. e. of Smyrna, *Rollins 55174* (GH). Williamson County: near Arrington Creek, ½ mi. s.e. of Arrington, *Rollins 55116* (GH); near Arrington Creek, ca. 7 mi. n. of College Grove, *Rollins 55117* (GH); roadside, 1 mi. n. of Kirkland, *Rollins 5517* (GH); near Mill Creek, 3 mi. n. of Nolensville, *Rollins 55110* (GH); 2.5 mi. n. of Triune, *Rollins 55111* (GH). Cheatham County: 3 mi w. of Ashland City, *Rollins 55151* (GH); flood plain of Cumberland River, 10 mi. n.w. of Ashland City, *Rollins 55156* (GH); near Pleasant View, *Quarterman & Stauffer 4948* (GH). Davidson County: flood plain of South Harpeth River near Linton, *Rollins 53134* (GH).

Of the fifty-four mounted specimens of *L. Lescurii* assembled from various herbaria for study, and excepting my own specimens, all but two were collected within the city of Nashville. Actually, the species is abundant in many localities in the six counties of the northern portion of the Central [Nashville] Basin of Tennessee. It seems strange that documentation for the wider range now known is not available in herbaria.

L. Lescurii appears early in the season, sometimes beginning to flower in early March, but most often it is at its flowering peak in April. Whole hillsides or open fields may be covered by a dense stand of the plants. This species seems to thrive equally on the flood plains of the river valleys and on the thin soil of open cedar glade-like areas of the hill slopes.

The branched trichomes present on the interior of the valves have not been seen by previous students. This feature is rare in the Cruciferae, but is now known in several species of *Lesquerella* including *L. perforata* where it was first noticed in the genus (Rollins, 1952). The long bulbous trichomes of the exterior valve surfaces are distinctive as may be seen in plate 1207. These trichomes are attached to a pedicel of tissue that projects above the valve wall. An understory of small branched

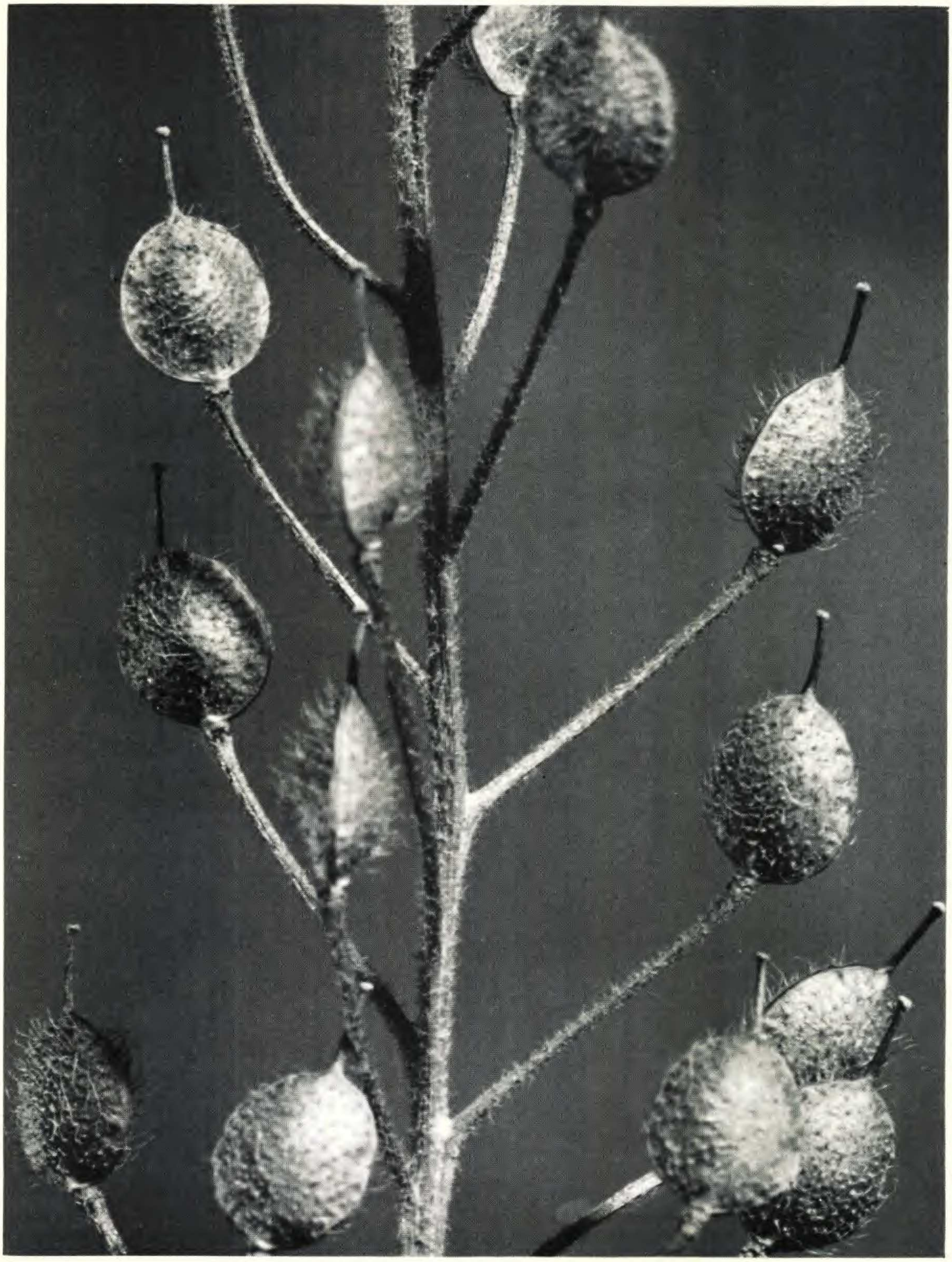

PLATE 1207. *Lesquerella Lescurii*. Part of an infructescence, ×6 (*Rollins 55174*). Photo by Frank White.

PLATE 1208. *Lesquerella densipila.* Part of an infructescence, ×6 (*Rollins & Quarterman 55146*). **Photo by Frank White.**

trichomes is present on young fruits, but these are often shed as the siliques mature.

There is considerable variation from plant to plant in any given population of *L. Lescurii* and trends of variation in different populations are sometimes recognizable. The intrapopulation variation is most frequently quantitative and may often be associated with local environmental factors, such as depth of soil, exposure and moisture availability. If conditions for prolonged growth are not present, a given plant may be small in stature and cease flowering after the setting of a few fruits. However, if factors are favorable, growth continues and the fruiting racemes become considerably elongated. The largest plants are found on the deep soils of the flood plains.

The taxonomic history of *L. Lescurii* reflects the doubts of Gray as to its rightful generic position. He was undoubtedly led to refer this species to *Vesicaria* in the beginning because other species of *Lesquerella* were being referred there by Hooker and other European botanists. The flattened siliques must have finally influenced him to move it into *Alyssum*, but it was equally out of place there as Watson finally showed. *L. Lescurii* has now been crossed artificially with *L. densipila* and *L. perforata* and it hybridizes naturally with *L. densipila*.

3. **Lesquerella densipila** Rollins, Rhodora **54:** 186. 1952.

Annual; stems several to numerous, erect or the outer decumbent at base, simple or branched, purplish below, 1–4 dm. high, hirsute below with spreading simple trichomes, rachis of inflorescence and upper portion of stems hirsute with smaller less spreading and frequently branched trichomes; basal leaves petiolate, lyrately pinnatifid to pinnately lobed, obtuse, 4–8 cm. long, 1–1.8 cm. wide, terminal lobe comparatively large, lateral lobes decurrent on rachis, hirsute on upper surface with mostly simple trichomes, lower surface with a mixture of large simple and smaller branched trichomes; cauline leaves sessile, auriculate, broadly ovate to oblong, 1–3 cm. long, 0.5–1.5 cm. broad, lower broadly obtuse, upper smaller and tending toward acuteness, dentate to nearly lobed, hirsute on both surfaces with mostly simple spreading trichomes; inflorescence racemose, 1–2 dm. long; fruiting pedicels divaricately ascending, straight, expanded at summit, 1–2 cm. long, pubescent with a mixture of simple and branched trichomes; sepals yellowish, nonsaccate, sparsely to generally covered with appressed branched trichomes, often with spreading single trichomes in addition, oblong, alternating members flat and boat-shaped, narrowed toward apex but remaining rounded, 2.5–4 mm. long, 1.5–2 mm. wide; petals yellow, broadly obovate, not markedly differentiated into

blade and claw, 6–8 mm. long, 4–5 mm. wide; filaments strongly dilated at base, attached to anthers just below middle, anthers nearly versatile, not sagittate, ca. 1.5 mm. long; glandular tissue in a thin continuous mold beneath stamens, forming projections between single and paired stamens and an abbreviated ring around the base of the filament of the single stamens; siliques subglobose to slightly broader than long, uncompressed, 3–4 mm. in diameter, densely pubescent with minute simple or forked spreading trichomes; styles 2–3 mm. long, pubescent sometimes, glabrous above, slightly expanded into a capitate stigma; 2–4 ovules in each loculus, funiculi free except at their very base; septum entire; replum nearly orbicular, pubescent; seeds margined, flattened, orbicular to slightly longer than broad, brown, 2–2.5 mm. in diameter; cotyledons accumbent; radicle short. N = 8. Plate 1208.

Tennessee. Rutherford County: 4 mi s.e. of Murfreesboro, *Rollins & De Selm 55122* (GH); near West Fork of Stone's River, 1.3 mi. s.w. of Bethel, *Rollins & De Selm 55124* (GH); near West Fork of Stone's River where state route 102 crosses, *Rollins & Bold 55134* (GH); floodplain of the Harpeth River, 1 mi. n. of Eagleville, *Rollins 5526* (GH). Bedford County: roadside near Alexander Creek, 2 mi. n. of the North Fork of Duck River, *Rollins 5537* (GH). Williamson County: 1 mi. n. of College Grove, *R. C. & D. Rollins 5215* (GH); ½ mi. n. of Kirkland, between Triune and College Grove, *Rollins 5315* (GH); same locality, *Rollins 5518* and *55112* (GH); Kirkland, *Rollins 53138* (GH); 3 mi. s.e. of Kirkland, *Rollins 5519* (GH); 6 mi. n. w. of College Grove near the Harpeth River, *Rollins 5514* and *55114* (GH). Marshall County: Duck River bottom, north of Verona, *Sharp, Felix and Adams 11187* (GH, type; UT, isotype); 1 mi. n. of Chapel Hill, *Rollins 5319* (GH); near Duck River, 3 mi. s. of Chapel Hill, *R. C. & D. Rollins 5217* (GH); ½ mi. s. of Duck River, ca. 5 mi. s. of Chapel Hill, *Rollins 5321* (GH). Maury County: flood plain of the Duck River, 10 mi. n.w. of Lewisburg, *Rollins 5539* (GH); open field and cedar glade, 4 mi. w. of Columbia, *Rollins 55108* (GH); same location, *Rollins and Quarterman 55146* (GH).

Though originally thought to be extremely local in its occurrence, *L. densipila* now proves to have a range in area approaching that of *L. Lescurii*. Recent collections from Rutherford, Bedford and Maury Counties provide the evidence for a considerably enlarged geographic area as compared to that known at the time the species was described in 1952. The species is confined to the Central Basin of Tennessee with its predominance of limestone soils.

The populations of *L. densipila* usually consist of a large number of individuals often numbered in the tens of thousands. These may be in open glade-like areas or along the river and stream bottoms which are subjected to spring flooding each year. As in *L. Lescurii*, there is considerable variation between individuals and between populations. These are principally

single character variations which can be seen from plant to plant, but there are few correlated differences between individuals of the same populations. Thus, independent assortment of genetic characters seems to be the rule. *L. densipila* is largely self incompatible, thereby insuring a continuing intermixing of the genes of any given population. Where different populations are involved, there are some minor correlated characteristics. However, *L. densipila* is an easily recognized species, and the characters that make it distinguishable from other species are present in every population. The exception to this comes in the hybrid populations that result from the natural crossing of *L. densipila* and *L. Lescurii* and of *L. densipila* and *L. stonensis.*

Lesquerella densipila and *L. Lescurii* come together at the junction of Arrington Creek, where the latter is found in abundance, and the Harpeth River, where *L. densipila* is abundantly found. From the entrance of Arrington Creek on down the Harpeth River, there are numerous populations of hybrids that have resulted from the crossing of these species. In these, the variation is very wide and the characters, for the most part, segregate independently. The fruit shape on most of the plants is somewhere between that of being extremely flattened which is characteristic of *L. Lescurii* and the globose type that is found in *L. densipila.* Occasional hybrid plants have flattened siliques, and in occasional ones the siliques are globose. The latter may be hirsute with very long trichomes, and the flattened type may lack simple trichomes altogether thus combining in different ways these characters of both species. In like manner, many other characteristics are combined in a complex series. Data supporting these conclusions have been given previously (Rollins, 1954).

Natural hybridization between *L. densipila* and *L. stonensis* has not been previously demonstrated, and the facts are at present being worked out. *Lesquerella densipila* var. *maxima* was based on hybrid plants from a population on Stones River whose variation was recognized, but was inexplicable at the time of publication. Now sufficient field work has been done to show that *L. densipila* is present on the West Fork of Stones River and some of the smaller tributaries to it. *L. stonensis*

is so far known only from the East Fork of Stones River. These two species meet at the junction of the east and west forks of the river, and from that point down river hybrid populations are produced which apparently quickly incorporate the genetic makeup of stray plants of either species that come within range of cross pollination. The hybrids of *L. densipila* × *L. stonensis* have previously been referred to under the name *L. densipila* var. *maxima*.

4. **Lesquerella lyrata** Rollins, sp. nov.

Annual, stems one to several, usually simple, erect, outer decumbent at base, 1–3 dm. long, densely hirsute below with simple spreading trichomes, upwards becoming a mixture of large simple and smaller branched trichomes with the small branched trichomes predominating above; basal leaves petioled, lyrate, 2–7 cm. long, 6–15 mm. wide, hirsute with simple trichomes or with a mixture of small branched and large simple trichomes, terminal lobe large and orbicular to elliptical; cauline leaves sessile, auriculate, clasping, ovate to broadly oblong, obtuse, nearly entire to coarsely dentate, 5–20 mm. long, 4–10 mm. wide, densely to sparsely hirsute with simple or simple and branched trichomes; inflorescences dense; pedicels slender, straight, divaricately ascending, densely pubescent, 1–1.5 cm. long; sepals pubescent, spreading and yellowish at anthesis, oblong, 3–4 mm. long, 1.2–1.5 mm. wide, outer pair very slightly saccate at base; petals yellow, broadly obovate, 5–7 mm. long, 3.5–4 mm. wide, slightly rounded, truncate or shallowly retuse at apex, limb short; glandular tissue subtending paired stamens, surrounding single stamens; paired stamens ca. 4 mm. long, single stamens ca. 3 mm. long; filaments dilated at base, those of paired stamens 3–3.5 mm. long, those of single stamens 2–2.5 mm. long; siliques depressed globose to subglobose, often slightly depressed at base of style and slightly didymous, glabrous, sessile, 2.5–3 mm. high, 3–4 mm. broad; styles slender, glabrous 1–1.5 mm. long; stigma unexpanded, nearly same diameter as style; replum orbicular to slightly broader than high; ovules 2–4 in each locule, funiculi free; seeds flattened, oval to nearly orbicular in outline, margined, brown, variable in size, 1.5–2.5 mm. on longest dimension, larger seeds in capsules with 2 per locule; cotyledons accumbent. N = 8. Plate 1209.

Herba annua; caulibus erectis vel decumbentibus simplicibus vel rare ramosis hirsutis 1–3 dm. longis; foliis radicalibus lyratis petiolatis hirsutis 2–7 cm. longis, 6–15 mm. latis; foliis caulinis sessilibus auriculatis oblongis vel ovatis obtusis pubescentibus dentatis vel integris 5–20 mm. longis, 4–10 mm. latis; pedicellis ascendentibus divaricatis pubescentibus, 1–1.5 cm. longis; sepalis flavis oblongis pubescentibus 3–4 mm. longis; petalis luteis late obovatis 5–7 mm. longis, 3.5–4 mm. latis; siliquis subglobosis depressis glabris 2.5–3 mm. altis, 3–4 mm. latis; stylis tenuibus glabris 1–1.5 mm. longis; loculis 2–4-ovulatis; seminibus marginatis brunneis compressis; cotyledonibus accumbentibus.

Alabama. Franklin County: cedar glade, roadside and field, near Richardson's Crossing, 7 miles east of Russellville, April 16, 1955, *Reed C. Rollins*,

George R. Cooley and L. J. Brass 5599 (GH, type); same location, April 5, 1955, *Rollins 5548* (GH); same location, April 27, 1955, *Rollins 55188* (GH); bottom land of creek, 4 miles north of Richardson's Crossing, about 9 miles east of Russellville, April 27, 1955, *Rollins 55187* (GH). Franklin-Moulton County line: roadside near cedar covered hill, 1.5 miles east of Newburg, April 5, 1955, *Rollins 5547* (GH).

Lesquerella has not heretofore been known from Alabama. However, I was led deliberately to look for it there because of the close parallel in the over all distribution pattern of the most easterly auriculate species of *Lesquerella* and of the genus *Leavenworthia*. The latter has been known from several stations in northwestern Alabama for some time. It seemed probable that if *Lesquerella* did occur between Tennessee and Texas, it would be on limestone or soils of limestone origin. The *Leavenworthia* stations in Moulton and Franklin Counties were picked as target areas for the search. *Lesquerella* was first found on April 5th near the Moulton-Franklin County line, as I proceeded westward on Alabama State Route 24. Here there was a small population of a few dozen plants extending along the roadside for about fifty yards. The glabrous fruits immediately indicated this *Lesquerella* was not the same species as any of those known from Tennessee, although the auriculate cauline leaves left no doubt about its being related to them. However, there remained the possibility that it was an outlying station of *L. auriculata* a species found chiefly in Oklahoma, but extending into Texas. My enthusiasm was aroused and I began to search in all directions to find additional populations. As the area of my search grew larger, I moved gradually west beyond the small village of Newburg, but no new populations were encountered until Richardson's Crossing was reached. At this location, marked by a lone roadside building housing the Richardson family and a general store, *Lesquerella* was found in abundance. This population, occurring with *Leavenworthia*, *Sedum* and similar cedar glade inhabiting plants, extended over a sizeable area of the glade itself, spilling up onto the roadside and over much of an adjacent old cotton field. Here was adequate material for field study, a mass collection and cytological fixations. On April 16th I had the pleasure of showing this station to Mr. George R. Cooley and Mr. L. J. Brass, at which time the type series was collected.

Lesquerella lyrata is most nearly related to *L. densipila* on the one hand and to *L. auriculata* on the other. The siliques are on the average smaller than in either of these species, being much smaller than in *L. auriculata*. Both the latter and *L. lyrata* have glabrous siliques, but they are fundamentally separated by ovule number. In *L. auriculata* there are from 12 to 20 ovules in each silique, while in *L. lyrata* there are only 4 to 8. The basal leaves are quite different in the two. Those of *L. auriculata* are often spatulate and nearly entire but there is variation to a sinuate dentate leaf similar to that of *L. grandiflora*. However in all of the material I have seen, the basal leaves of *L. lyrata* are definitely lyrate with a large terminal obtuse lobe and much reduced more or less acute lobes or teeth along the margins.

Aside from ovule number, perhaps the most noticeable differences between *L. auriculata* and *L. lyrata* are in silique size and shape. In the former, the siliques are longer than broad, elliptical in outline, with a rounded apex, while in the latter they are broader than long and often with a slight depression at the base of the style. As to size, the fruit of *L. lyrata* measures 2.5–3 mm. high, whereas in *L. auriculata*, it ranges from 4–6(–8) mm. high. The stigma is rather strongly expanded in *L. auriculata* being at least twice the diameter of the style. In *L. lyrata*, the stigma is very slightly expanded beyond the style diameter itself.

The siliques of *L. lyrata* are only slightly smaller than in *L. densipila* and they are of the same general shape although perhaps more markedly depressed globose to nearly didymous than in the most extreme populations of the latter. Also, the ovule number runs about the same in the two species, so far as extremes are concerned. No data have been assembled on the point but I have the impression that 7 or 8 ovules per silique occur most frequently in *L. densipila* while the most frequent number in *L. lyrata* is 4. The one very marked difference between these species is the indument on the exterior of the siliques and on the styles. In *L. lyrata*, both are perfectly glabrous. In *L. densipila*, the exteriors of the siliques are densely pilose with minute trichomes and the styles are hirsute.

All of the known facts of morphology point to a closer relationship between *L. densipila* and *L. lyrata* than between the latter

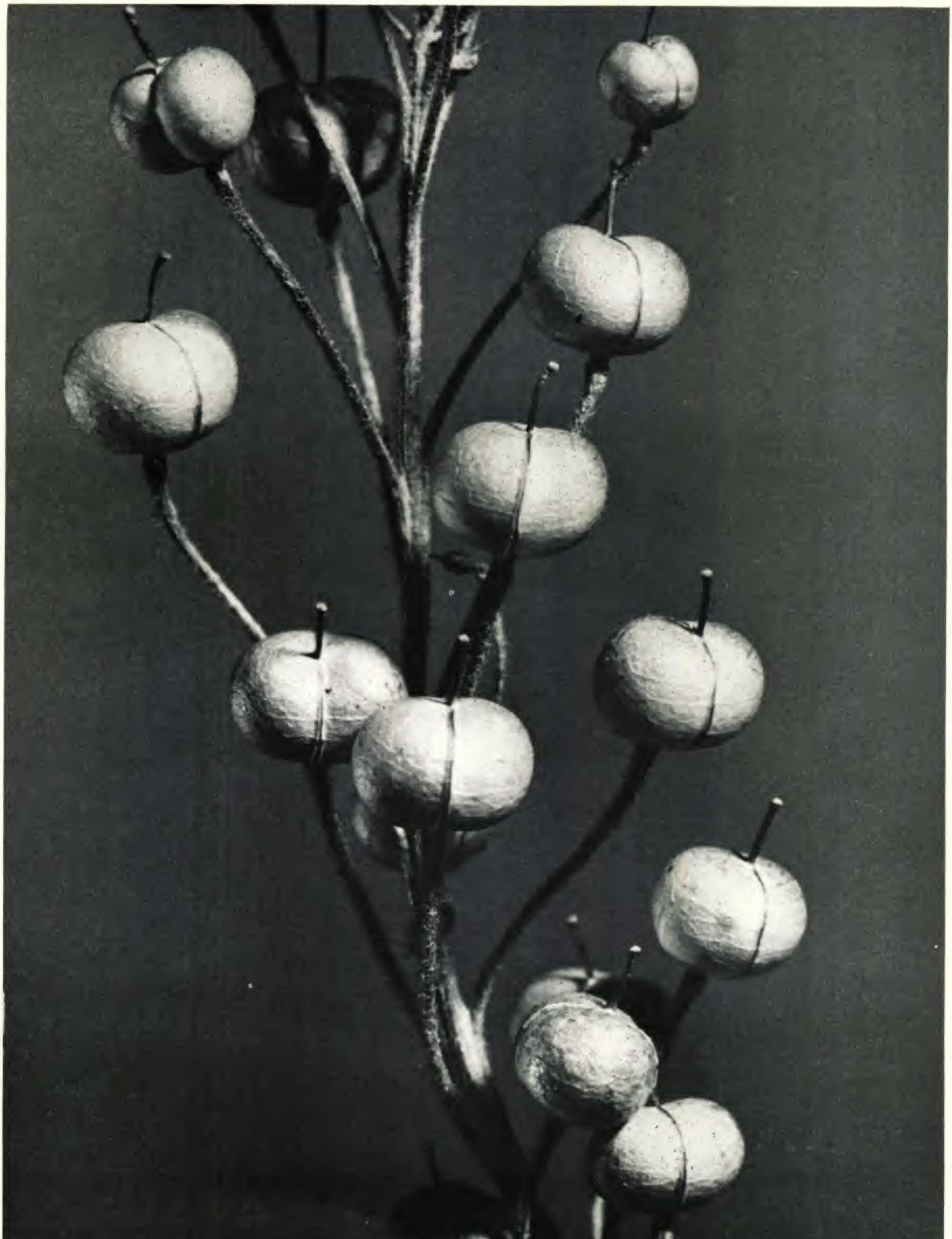

PLATE 1209. *Lesquerella lyrata.* Part of an infructescence, ×6 (*Rollins, Cooley & Brass 5599*). Photo by Frank White.

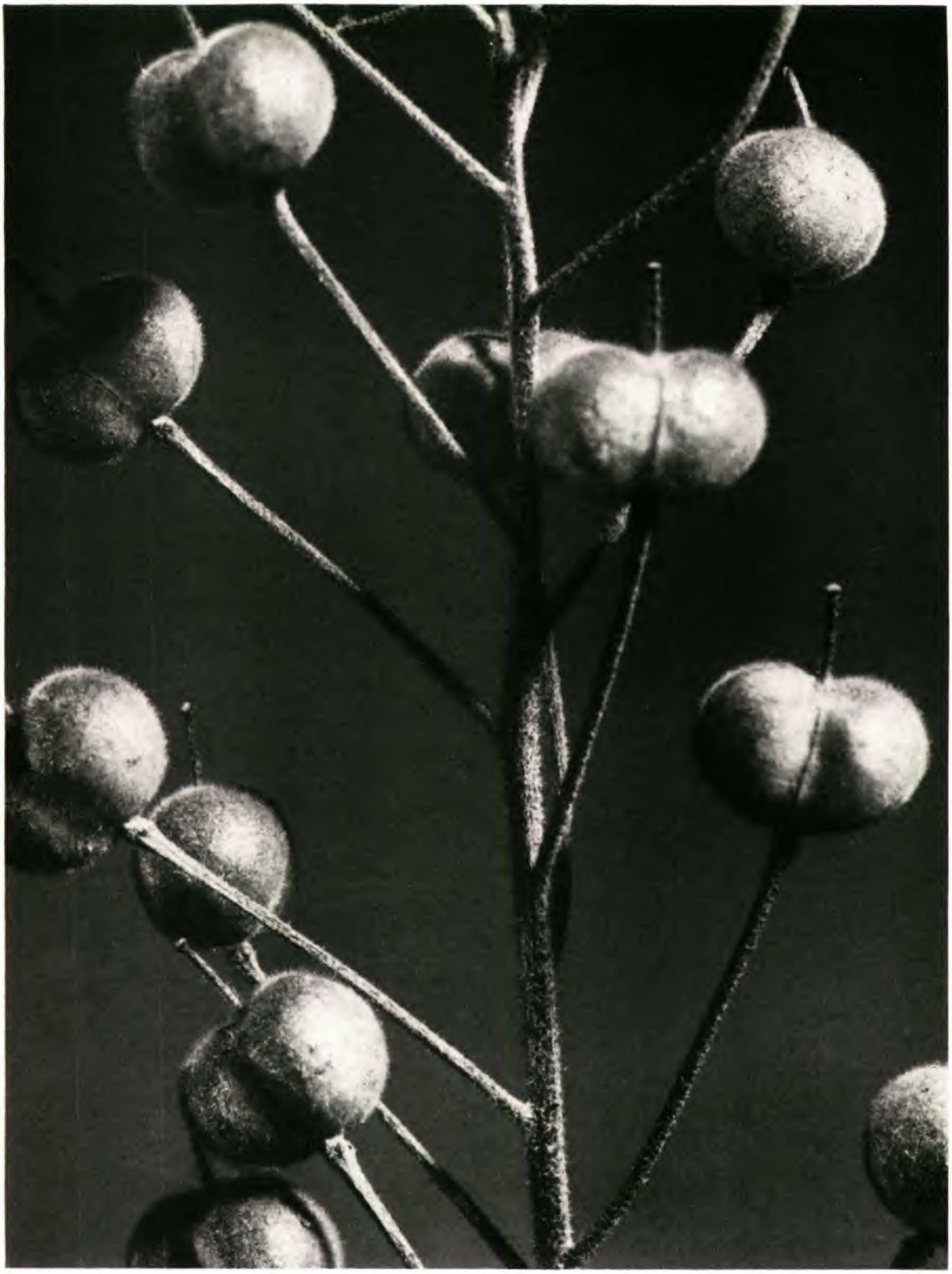

PLATE 1210. *Lesquerella stonensis.* Part of an infructescence, ×6 (*Rollins, 55176*). Photo by Frank White.

and *L. auriculata*. This presumed affinity has not been tested experimentally. The chromosome numbers of all three are the same, n = 8.

5. **Lesquerella stonensis** Rollins, sp. nov.

Annual, stems several from the base, simple or usually branched, 2–4 dm. long, erect, the outer usually decumbent at base, densely hirsute with simple trichomes below, densely pubescent above with simple or a combination of simple, forked and more lightly branched trichomes; basal leaves petioled, lyrately lobed to pinnatifid, obtuse, 3–6 cm. long, 8–15 mm. wide, densely hirsute, simple trichomes present on upper surface, a mixture of long simple and shorter forked or branched trichomes present on lower surface, lobes variable, terminal lobe large and ovate to nearly orbicular, entire to sinuate dentate, lateral lobes triangular to broadly oblong, obtuse, decurrent on the leaf rachis; cauline leaves sessile, auriculate, clasping, broadly oblong to ovate dentate, 1–5 cm. long, 5–15 mm. wide, lower cauline leaves densely hirsute with predominantly simple trichomes on upper surface, a mixture of simple, forked and branched trichomes on lower surface, upper cauline leaves densely pubescent with predominantly forked or branched trichomes; infructescence 8–15 cm. long, rachis densely pubescent with mostly branched or forked trichomes; pedicels straight or nearly so, divaricately ascending, densely pubescent, 1–2.5 cm. long; sepals oblong to nearly ovate, narrowed toward apex, pubescent, 4.5–5.5 mm. long, 1.5–2 mm. wide, outer pair slightly saccate, inner pair narrower and nonsaccate; petals white with a yellowish short claw, obovate, rounded to emarginate at apex, 7–9 mm. long, 5–6 mm. wide; filaments dilated at base, those of the paired stamens 4–4.5 mm. long, those of single stamens 3–3.5 mm. long; glandular tissue continuous, surrounding insertion point of single stamens, subtending insertion point of paired stamens; siliques depressed globose to slightly didymous, densely hirsute with simple trichomes, 4–5 mm. broad, 3–4 mm. high; edge of replum hirsute, not raised above valve margins; valves glabrous on interior; styles hirsute at least below, slender, ca. 2 mm. long; stigma expanded; replum orbicular to slightly wider than long, rounded at apex; septum usually perforate, sometimes entire, perforation variable in size; funiculi not attached to septum; ovules 4–6 in each locule; seeds dark brown, flattened, oval in outline, margined, 1.8–2 mm. long, ca. 1.5 mm. wide; cotyledons accumbent. Plate 1210.

Herba annua, caulibus ramosis vel rare simplicibus erectis vel decumbentibus hirsutis 2–4 dm. altis; foliis radicalibus petiolatis lyratis hirsutis 3–6 cm. longis, 8–15 mm. latis; foliis caulinis sessilibus auriculatis dentatis oblongis vel ovatis 1–5 cm. longis, 5–15 mm. latis; pedicellis divaricatis pubescentibus 1–2.5 cm. longis; sepalis oblongis vel ovatis pubescentibus 4.5–5.5 mm. longis, 1.5–2 mm. latis; petalis albis obovatis 7–9 mm. longis, 5–6 mm. latis; siliquis subglobosis depressis dense hirsutis 4–5 mm. latis, 3–4 mm. altis; stylis hirsutis ca. 2 mm. longis; loculis 4–6-ovulatis; seminibus marginatis, brunneis compressis 1.8–2 mm. longis, ca. 1.5 mm. latis; cotyledonibus accumbentibus.

Tennessee. Rutherford County: field and flood plain, East Fork of Stones River, Walterhill, April 26, 1955, *Reed C. Rollins 55176* (GH, type); same location, April 1, 1955, *Rollins 5507* (GH); pasture and hilltop, near East Fork of Stones River, 4½ mi. n.w. of Walterhill, April 1, 1955, *Rollins 5508* (GH); east of Old Jefferson near point where state route 102 crosses East Fork of Stones River, April 22, 1955, *Reed C. Rollins and Harold Bold 55138* (GH); pasture near East Fork of Stones River, 1 mi. s.w. of Lascassas, April 26, 1955, *Rollins 55177* (GH).

The variability of populations of *Lesquerella densipila* var. *maxima* noticeable in the field first suggested that these were of hybrid origin. In publishing this variety (Rollins, 1952) I called attention to the divergence in trichome length on different plants of the same population. Later, in working up data compiled in seeking to discover species that might have figured in the origin of var. *maxima*, it became clear that while *L. densipila* was probably involved as one parental species, there was no known species in the Central Basin of Tennessee that could have played the role of the other parent. There were characters such as fruit shape, trichome size and trichome distribution that could not have arisen from *L. densipila* or any other known species. In the spring of 1955, working on the hypothesis that the plants of var. *maxima* were of hybrid origin and that an unknown *Lesquerella* was involved in producing these hybrid plants, I sought to find the unknown. *L. stonensis* is that heretofore unknown species.

The situation with regard to the hybrid origin of var. *maxima* is now fairly clear, though a complete study has not been made, up to the present. *Lesquerella stonensis* exists as a pure species at various localities along the East Fork of Stones River. *L. densipila* exists as a pure species on the West Fork of Stones River and to the south and west of this area in the Central Basin. Both species occupy flood plain habitats and presumably their most important direction of movement is downstream, the seeds being carried during the annual spring floods. The two species come together where the two forks of Stones River meet and hybridization takes place there. From the junction of the East and West Forks downstream, all of the populations examined showed evidences of their hybrid origin.

Lesquerella stonensis is a white flowered species, most closely related, as shown by most of its characteristics, to the yellow flowered *L. densipila*. It differs not only in flower color from

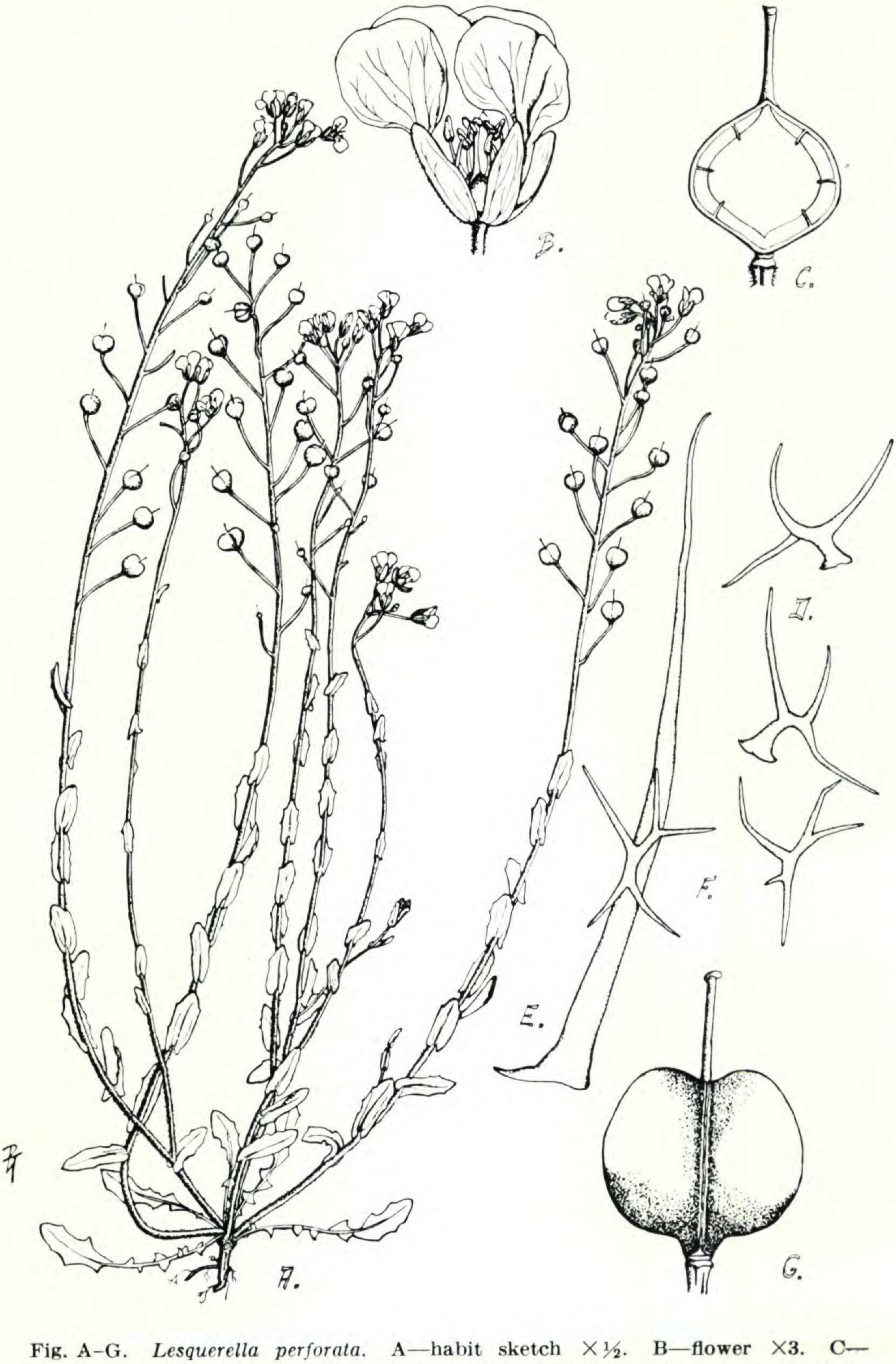

Fig. A–G. *Lesquerella perforata.* A—habit sketch ×½. B—flower ×3. C—replum and perforate septum ×4. D–F—trichomes of the stems and leaves ×125. G—silique ×4. Drawings by B. Tugendhat.

L. densipila but also in the size and shape of the siliques and in the length of the trichomes on the valves of the siliques. In *L. stonensis*, the larger fruits are depressed globose to slightly didymous while the smaller fruits of *L. densipila* are globose to subglobose. On the valve surfaces, a dense covering of minute simple or forked trichomes is present in *L. densipila*, but in *L. stonensis* the simple trichomes are much longer and form a less dense indument. By comparing plate 1210, *L. stonensis*, and plate 1208, *L. densipila*, which are reproduced at the same scale of magnification, the differences of indument between these species can readily be seen. Most of the siliques of *L. stonensis* examined possessed a perforate septum. Sometimes the perforation was small. However, in many instances it was larger, ranging upward in size to about one-fourth of the total area of the septum.

6. **Lesquerella perforata** Rollins, Rhodora **54:** 190. 1952.

Annual; stems several to many, outer usually decumbent at base, inner erect, simple or branched, 1 dm. high, densely hirsute below with large spreading mostly simple trichomes, pubescent above with less-spreading mostly branched trichomes; basal leaves lyrately lobed, petiolate, 2–5 cm. long, 5–15 mm. wide, lobes variable, terminal lobe orbicular to ovate, entire or dentate, obtuse to more pointed, lateral lobes broadly oblong, entire or shallowly toothed, becoming remote toward petiole; hirsute on both surfaces, with mostly simple trichomes, marginal trichomes smaller and branched; cauline leaves sessile, auriculate, broadly oblong to nearly ovate, sagittate, dentate, 8–20 mm. long, 4–8 mm. wide, hirsute above with simple trichomes, below with a mixture of simple and branched trichomes; pedicels straight, divaricately ascending, scarcely swollen at apex, 6–12 mm. long, uniformly pubescent with branched trichomes or with a mixture of simple and branched trichomes; sepals oblong, pubescent with a mixture of large and small branched trichomes, 3.5–5 mm. long, 1.5–2 mm. wide; petals white to pale lavender with a yellowish claw, sometimes tinged with light purple when dry, unguiculate, obovate to very broadly spatulate, emarginate to nearly entire, 7–9 mm. long, 5–6 mm. wide; filaments dilated at base, those of paired stamens 4–4.5 mm. long, anthers ca. 1.3–1.5 mm. long; glandular tissue subtending all filaments and nearly surrounding those of the single stamens, with projections between single and paired stamens; siliques inflated, variable in shape, broadly obovoid to subpyriform, very slightly stipitate, sparsely hirsute with large simple or forked trichomes to nearly glabrous on the exterior, densely pubescent with small dendritically branched trichomes on the interior, 4–6 mm. long, widest above the middle, 4 mm. wide; septum nearly obsolete, represented by

only a narrow band of tissue around the inner margin of the replum; styles 1.5–.5 mm. long, unexpanded or only very slightly expanded at apex; ovules 2–6 in each loculus, funiculi nearly free, seeds slightly longer than broad to nearly orbicular, flattened, margined, 1.5–2.5 mm. long, 1.2–2 mm. broad; cotyledons accumbent. N = 8. Plate 1211.

Tennessee, Wilson County: open field near Spring Creek, 5 mi. n. of Lebanon, 1952, *R. C. & D. Rollins 5207* (GH); same general locality, 1953, *Rollins 5304* (GH); same locality, 1955, *Rollins & Bold 55139* (GH); near Lebanon, *Sharp 83* (TENN); western edge of Lebanon, *R. C. & D. Rollins 5208* (GH); near Barton Creek, ½ mi. w. of Lebanon, *Rollins 5306, 53145* (GH); 3 mi. w. of Lebanon, *Rollins & Bold 55141* (GH).

Aside from the perforate septum and the very dense covering of dendritic trichomes on the interior of the valves which I have emphasized before, l.c., one of the striking features of this species is the papery quality of the siliques. As may be seen in plate 1211, the valves are somewhat wrinkled and unusually strongly veined. These are not raised veins, but they do have greater density than the papery valve itself. The replum margin stands above the level of the adjacent valves which flare slightly outward on each side of it. Thus, the edge of the replum together with the valve margins forms a definite ridge that nearly encircles the silique.

Mass collections of fruiting racemes have been available for study, and one of the very noticeable things about the plants of a population of *L. perforata* is the variation in the shape of the silique. In some plants, the siliques are definitely pyriform, in others nearly the shape of an inverted triangle, and in still others the siliques are much depressed and almost didymous. Also, there appears to be a difference in ovule number between two populations. In ten plants from the population near Spring Creek represented by No. 55139, there was an average of 3.1 ovules per locule. Ten plants of the population three miles west of Lebanon, No. 55141, had an average of 5.0 ovules per locule. The significance of these and other differences between populations is not understood at present, but I shall not be surprised if further study eventually shows that this and other species of *Lesquerella* of the Central Basin are in the process of fractionating, evolutionally speaking, to produce a new array of forms that may eventually become quite distinct.

Lesquerella perforata is apparently local in its occurrence, but I suggest this with considerable caution. In three different

years, I have searched the general area around Lebanon for populations of *Lesquerella* hoping to discover a broader range for *L. perforata*. On each occasion, the species was found in great abundance at the known stations, but these are all within six miles of Lebanon. Attempts to find it farther afield were not successful. However, my experience with *Lesquerella* elsewhere in the Central Basin of Tennessee leads me to be cautious about stating a definite range for a given species. At first, *L. densipila* was thought to be from a very limited area, but now, as a result of recent field work, it is known to be quite widespread in the Central Basin.

7. **Lesquerella auriculata** (Engelm. & Gray) Watson, Proc. Am. Acad. **23:** 250. 1888.

Vesicaria auriculata Engelm. & Gray, Bost. Journ. Nat. Hist. **5:** 240. 1845.

Alyssum auriculatum (Engelm. & Gray) Kuntze, Rev. Gen. Pl. **2:** 931. 1891.

Annual; stems several to many, erect or decumbent at base, simple, 0.5–2 dm. high, rather stout, hirsute with long simple trichomes and with an understory of smaller branched trichomes; basal leaves with a short petiole, lyrate to sinuate dentate, sometimes nearly entire, usually obtuse, rarely somewhat acute, 2–5 cm. long, 8–15 mm. wide, hirsute on margins, midrib, and much of upper surface with simple trichomes, upper and lower surfaces often pubescent with smaller branched trichomes; cauline leaves auriculate, sessile, entire to dentate, usually overlapping on the stem, oblong to sagittate, 1–4 cm. long, 3–10 mm. wide; pedicels divaricately ascending to divergent at about 45°, nearly straight, hirsute with spreading simple and branched trichomes, 7–15 mm. long, not expanded at summit; sepals narrowly oblong, hirsute with spreading simple and branched trichomes, 4–6 mm. long, 1.5–2 mm. wide, outer pair slightly saccate, inner pair flat at base; petals yellow, obovate, entire to slightly emarginate at apex, 7–10 mm. long, 4–5 mm. wide; filaments abruptly dilated at base; siliques globose to longer than broad, glabrous, 4–6 (–8) mm. long, 4–6 mm. wide, nearly sessile, valves glabrous within; septum entire or rarely with a small perforation; styles glabrous, 1.5–2 mm. long; stigma expanded; ovules (4–) 6–8 (–10) in each locule; seeds nearly orbicular, flattened, margined, ca. 2 mm. in diameter; cotyledons accumbent. N = 8.

Oklahoma: 2 mi. so. Choteau, Mayes Co., *D. M. Moore 55–11* (GH); 6 mi. so. Ponco City, Kay Co., *Waterfall & McCoy 11402* (OKLA, TEX); 1 mi. w. Perry, Noble Co., *Harding 296 & 334* (OKLA); 4 mi. e. Stillwater, Payne Co., *Waterfall 9907* (OKLA, TEX); edge of Enid, Garfield Co., *Gephardt 16 & 160* (US); near Kingfisher, Kingfisher Co., *Stevens 188* (GH, MO, NY, OKLA, US);